THE STRUCTURE OF *VERTEBRARIA INDICA* ROYLE

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ABSTRACT. Pulls of carbonised substance of Royle's type of *V. indica* and 250 other axes referable to the same species have been studied. The other specimens were collected from the Raniganj and Giridih coalfields (Permian; Upper Damuda Group, Gondwana System). They all show the same kinds of secondary xylem, large parenchyma, and phloem-like cells. The different kinds of pitting and their frequency in the tracheids, the frequency of uniseriate rays of different heights, their length, and the range of variation in xylem character, have been determined. It has been found that characters of xylem described for *V. raniganjensis* are within the range of *V. indica* and this species may be regarded as a synonym of *V. indica*. None of our several axes of *V. indica* shows any trace of pith.

ROYLE (1833) founded two species of *Vertebraria* from India (*V. indica* and *V. radiata*), that were later recognized as lateral and sectional views of the same fossil. By a strange coincidence McCoy (1847) and Dana (1849) made the same error in giving two names (*V. australis* and *Clasteria australis*) to laterally exposed and sectional views respectively of the same fossil. Arber (1905) and others have pointed out that all axes of this kind belong to a single species, *Vertebraria indica*, but Surange and Maheshwari (1962) have recognized two new species of the genus among compressions and Schopf (1965) has established a fourth species for a petrified axis, described earlier by Kraüsel. However, a review of the literature on *Vertebraria* gave us the impression that the characters of the various species of the genus were neither sufficiently known nor clearly demarcated.

MATERIAL AND METHODS

A large number of specimens of *Vertebraria* were collected from localities in the coalfields of Raniganj and Giridih. About 300 celloidin pulls of coaly material were prepared from 250 compressions. The pulls were mounted in Canada balsam and examined in ordinary transmitted light under a compound microscope and also under phase contrast and dark field illumination. Averages have been generally calculated from 300 random counts but where this was not possible, the smaller number of counts has been mentioned against the averages.

All figured specimens and slides of this paper form part of Divya Darshan Pant Collection of plant fossils, located in the Botany Department of the Allahabad University.

DESCRIPTION OF EXTERNAL FEATURES

Compressions of *Vertebraria* axes are either found lying almost vertical to the bedding plane and seen in sectional views or they lie horizontally in the layers of the Lower Gondwana rocks and are exposed in a lateral view (Pl. 124, Pl. 125, figs. 1–2; text-fig. 1A–C). Sectional views of *Vertebraria* axes show rays of carbon, all joined and radiating from a centre and separated from each other by rather wide bays of rock matrix. The

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rays are simple and almost equal, their ends may be slightly flattened, occasionally the surface of a bay may be covered by a film of carbon which joins two adjacent rays (Pl. 125, fig. 1). The largest vertically preserved *Vertebraria* in our collection is 2·7 cm. in diameter. Lateral views of horizontally compressed *Vertebraria* axes are more common. The thickest specimen in our collection is 9 cm. wide. The axes show 2 to 4 series of rectangular areas with 1 to 3 intervening longitudinal furrows or ridges. As a rule the rectangular areas are of almost equal size but sometimes they may appear very unequal (text-fig. 1B). Branching axes are not uncommon. As described by Oldham (1897) the branching of these axes takes place in two ways. Either the branching axis divides into two or more almost equal branches or the axes produce thinner branches from their sides (text-fig. 1A–C). The branches may show similar rectangular areas but some of the thinner axes have a central longitudinal groove or ridge and only occasional obscure horizontal marks (Pl. 124, fig. 5). Some of these axes show attached roots (Pl. 124, fig. 3). An attached root is also seen in a vertically compressed axis (Pl. 125, fig. 1).

As suggested by Pant (1956) the preservation of horizontally compressed *Vertebraria* is not fundamentally different from that of vertically compressed axes, except that their xylem rays radiating dorsally and ventrally become shorter or narrower in the radial direction by undergoing greater radial compression, while the radial dimension of their horizontally placed rays remains practically uncompressed. Naturally such axes are usually exposed along the plane of easier splitting, i.e., along the wider horizontally placed rays and these appear as two series of typical rectangular areas on either side of a median ridge or furrow representing the central longitudinal core of *Vertebraria* and the transverse sides of the rectangles represent the upper and lower limits of the wide parenchymatous bays. Occasionally the rock is fractured along one of the dorsally or ventrally placed vertically compressed rays (Pant 1956, text-fig. 2A, where towards the top left a few narrower rectangular areas are those of a vertically compressed ray). Additional longitudinal rows of rectangular areas may be seen at a point where a *Vertebraria* branches (text-fig. 1B; Pl. 124, fig. 2). Many of our axes lie among leaves of *Glossopteris*, *Rhabdotaenia*, *Pteronilssonia*, and other specimens. In one of these a *Glossopteris* leaf at first sight appeared to be connected with a *Vertebraria* but a closer examination reveals that the apical end of the leaf was actually facing the axis.

INTERNAL STRUCTURE

Horizontally compressed axes

Celloidin pulls of carbon from horizontally compressed axes and their branches with or without typical rectangular areas usually show the same kind of secondary xylem as

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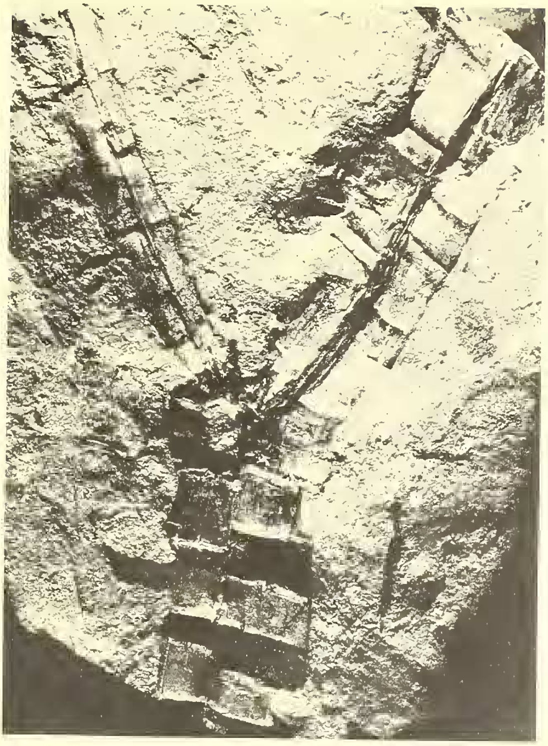
EXPLANATION OF PLATE 124

Figs. 1–5. *Vertebraria indica* Royle. 1, Forked axis, No. 1804, $\times\frac{6}{5}$. 2, Trifurcate axis showing wide rectangular areas in two series below and triseriate areas above; rectangular areas are not seen for some distance near the lower end; No. 1756, $\times\frac{2}{5}$. 3, Axis with elongated rectangular areas and a few thin branches (roots) with scalariform xylem (cf. *Lithorhiza tenuirama* Pant), No. 1805, $\times\frac{2}{5}$. 4, Fragment of a thick axis showing tetraseriate rectangular areas, No. 1808, $\times\frac{1}{2}$. 5, Axis with a median furrow but its rectangular areas are ill defined due to the presence of only a few rather obscure transverse marks, No. 3052, $\times\frac{4}{5}$.



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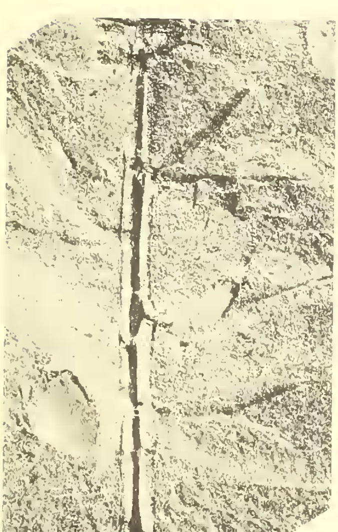

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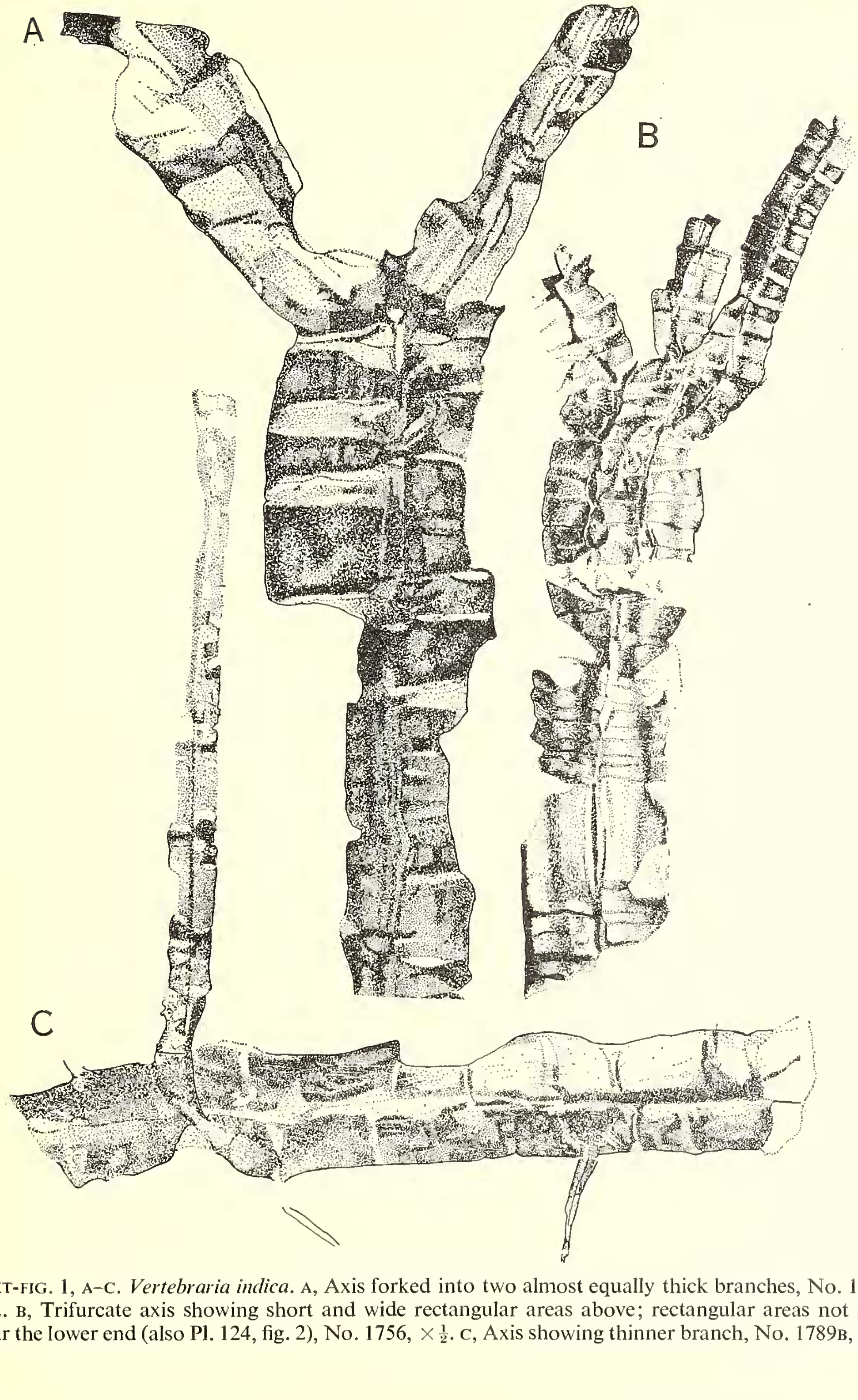
PANT and SINGH, Permian *Vertebraria*



TEXT-FIG. 1, A–C. *Vertebraria indica.* A, Axis forked into two almost equally thick branches, No. 1804, ×2. B, Trifurcate axis showing short and wide rectangular areas above; rectangular areas not seen near the lower end (also Pl. 124, fig. 2), No. 1756, ×½. C, Axis showing thinner branch, No. 1789B, ×2.

is seen in a radial section. Naturally, in compressed wood, such pulls also show the radial or tangential walls of the tracheids often overlapping each other. At a few places, the xylem is even seen in a tangential view or in a partially radial and partially tangential view (text-fig. 2H; Pl. 127, fig. 6).

Radial views of xylem. (*a*) *Royle's type*. A pull from Royle's type specimen No. V. 4189 in the British Museum (Natural History) shows the typical xylem of *Vertebraria* as if in a radial longitudinal section (Pl. 125, fig. 3). The tracheids have uniseriate to tri-seriate oval to circular pits placed far apart or contiguous. Biseriate and triseriate pits are usually opposite but alternately arranged pits have also been observed (text-fig. 3D, E). Rays are uniseriate and ray fields show pits usually without any border (text-fig. 3F). A few large parenchyma cells like those reported by Pant (1956) are mostly broken down.

(*b*) *Specimens from Raniganj and Giridih coalfields*. All our pulls of the carbon from horizontally preserved specimens of *Vertebraria* axes show well-preserved secondary xylem covering the entire surface of the rectangular areas (where carbon is preserved), from one side of the axis through the median ridge or furrow right up to the opposite side. On all our slides most of the xylem is seen as in a radial longitudinal section. A pith should have been visible in such radial views but no pull from the axes in our collection shows any trace of parenchyma cells in the centre, although ray parenchyma, phloem-like thin-walled cells and the typical large parenchyma cells of *Vertebraria* are usually well preserved. Instead, numerous pulls show undisturbed tracheids filling the central parts of the axes.

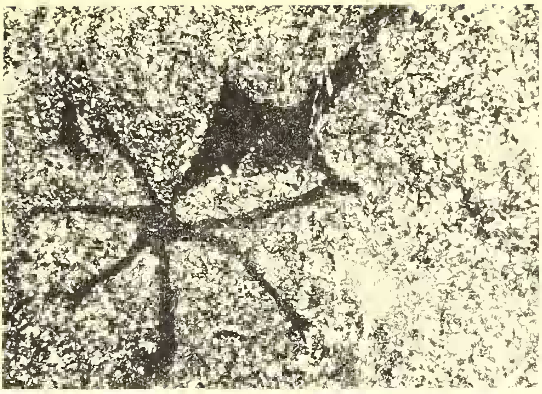
Primary xylem. Primary xylem tracheids consisting of scalariform, annular, or spiral elements were described from pulls of *Vertebraria* by Walton and Wilson (1932) and Pant (1956). Pant described them as occurring towards the periphery of the axes, where they could even have belonged to associated or attached roots.

Secondary xylem. The wood is mostly secondary and pycnoxylic. The tracheids are almost all of a uniform type without growth rings. The length of most tracheids is indeterminable in the pulls and this may suggest that they were usually longer than the size of our pulls. However, 60 complete tracheids have been observed; their length is 77–679 μ (average 250 μ, δ 105). As both ends of most tracheids are not seen, we presume that these sizes may represent the shorter elements in the xylem of *Vertebraria.* The width of the tracheids ranges from 10–56 μ (average width of tracheids is 31 μ, δ 20·5). The tracheidal walls are up to 4 μ thick. The ends of the tracheids taper gradually to a narrow point, the end walls being very oblique (Pl. 126, fig. 1). The tracheids over the rectangular areas on the surface of the axes are straight and vertical but in the region of the horizontal ridges or furrows they are slightly curved.

Arrangement of pits. The pits on radial walls are uniseriate, or multiseriate up to 5 series of pits (text-fig. 2 B, C, and G). A single tracheid with 6 seriate pits was also seen (text-fig. 2 E, Pl. 126, fig. 2).

EXPLANATION OF PLATE 125

Figs. 1–6, *Vertebraria indica* Royle. 1, Vertically compressed axis towards the top right-hand corner; part of transverse diaphragm (black) and an attached root also seen; No. 1375, ×11. 2, Vertically compressed axis showing marks of peripheral tissues, No. 1810, ×2. 3, Pull from Royle's holotype showing biseriate and triseriate pits and a two-cell high ray, V. 4189, ×300. 4, Xylem of root attached to axis in Plate 124, fig. 3, showing scalariform tracheids, Slide No. 1805, ×350. 5, Portions of tracheidal walls of axis showing crossed pit pores, Slide No. 1809 Ba, ×500. 6, Tracheids showing uniseriate pits or mixed uniseriate and biseriate opposite pits, Slide No. 1808C, ×800.



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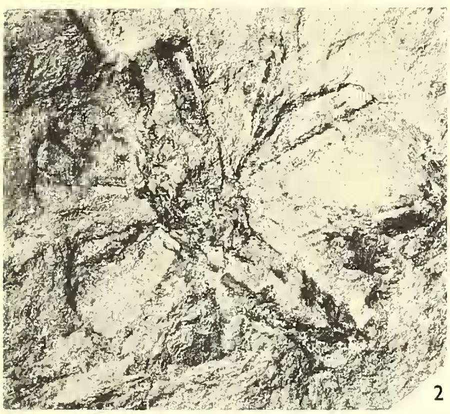

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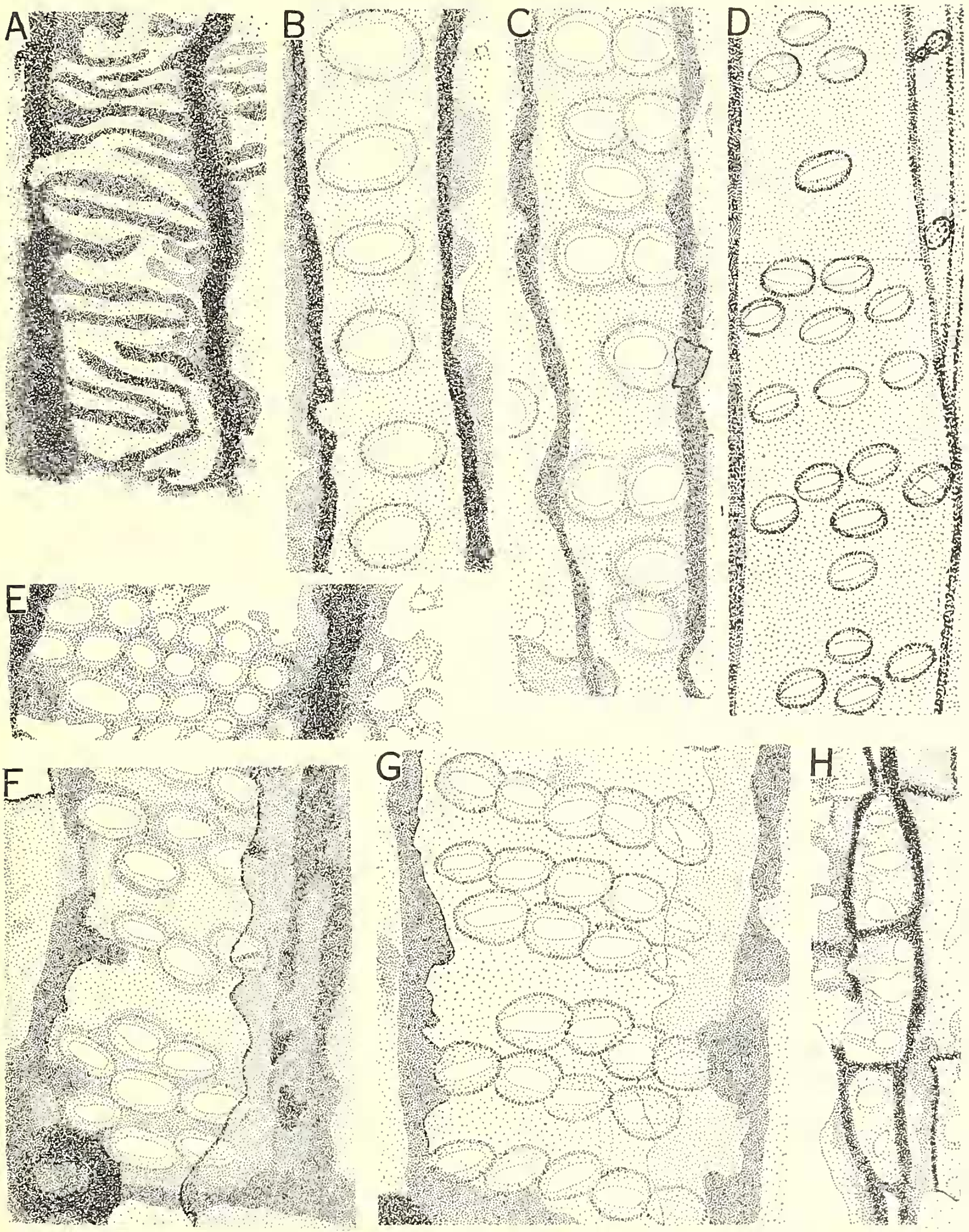
PANT and SINGH, Permian *Vertebraria*



TEXT-FIG. 2, A–H. *Vertebraria indica*. A, Portion of tracheid showing scalariform pitting (also Pl. 127, fig. 4); Slide No. 586, ×1,000. B, Part of tracheid with uniseriate non-contiguous pits; Slide No. 1784 Da, ×750. C, Portion of tracheid showing uniseriate and biseriate pits; Slide No. 1784 Da, ×750. D, Irregularly-pitted tracheid showing oval pit-pores, some with crossed pit-pores; Slide No. 1807A, ×1,000. E, Portion of wide tracheid showing 6-seriate pits (also Pl. 126, fig. 2); Slide No. 1807A, ×750. F, Portion of tracheid showing oval groups of pits with a central pit; Slide No. 1765 C2, ×750. G, Tracheid showing tetraseriate and pentaseriate pits; Slide No. 1767C, ×750. H, Uniseriate 3-cell-high ray in tangential view; Slide No. 1784 Da, ×450.

The pits may be contiguous or far apart (text-fig. 2 B; Pl. 125, fig. 5) and the portions of the same radial wall may be pitted in some regions and unpitted for varying distances in other regions. Multiseriate pits may be opposite, araucarioid (i.e. with crowded alternate pits having hexagonal outlines) or irregularly arranged (Pl. 126, fig. 3). As a rule unpitted portions of the wall are seen in tracheids with irregular pits. Some of these may show circular or oval groups of 3 to 9 pits (text-fig. 2 D, F). The same tracheid may show different kinds of pitting in different regions i.e., uniseriate or multiseriate, opposite or alternate, contiguous or non-contiguous (text-fig. 2 C; Pl. 125, fig. 6; Pl. 126, fig. 3). A random count of 300 tracheids showed about 11% with uniseriate pits, 47% opposite multiseriate pits, 12% alternate crowded multiseriate pits of araucarioid type, 28% irregular pits, and 2% showed portions of walls without pits. Out of the 47% tracheids with opposite pits 19% are biseriate, 18% triseriate, 8% tetraseriate, and 2% pentaseriate.

Shape and size of pits. The typical shape of bordered pits may be circular or oval (text-fig. 2 B). Oval pits in multiseriate tracheids are placed horizontally but where uniseriate they may be horizontal or oblique. The pit pores are generally oval but occasionally rounded. The two opposite pores of a pit pair are usually crossed (text-fig. 2D; Pl. 125, fig. 5). In the tracheids of the thinner axes pit pores are wide with a very thin border.

In some regions of the pulls, the tracheids show large horizontally extended oval pits where a border is not discernible. Such pits may be uniseriate or multiseriate. Where uniseriate they almost look like scalariform thickenings (text-fig. 2A; Plate 125, fig. 4; Plate 127, fig. 4) and where multiseriate they often appear transitional between typical scalariform and pitted elements. Pant (1956) described such tracheids as in contact with large parenchyma cells.

The circular pits are 4–8·5 μ (average 5 μ, δ 0·5). The length of the oval pits is 8·5–26·5 μ (average length is 13 μ, δ 2·5) and the breadth is 4–10 μ (average breadth is 6 μ, δ 1). The length of the oval pits whose borders are not clear is 10–31 μ (average length is 21·5 μ, δ 1·5) and the breadth is 4–10 μ (average breadth is 7 μ, δ 1).

Secondary xylem rays. Only uniseriate secondary xylem rays have been observed. These are 1–13 cells high (Pl. 126, fig. 5; Pl. 127, fig. 1), but more commonly they are only 1–4 cells high:

Percentage of uniseriate rays of differing heights

Height of rays in number of cells	1	2	3	4	5	6	7	13
Percentage	33	29	17	10	6	2	2	1

Frequency of rays per 10 mm.^{2} is 4–18 averaging 9 (60 readings, δ 4). The rays are 1–48 cells long (average 11 cells, δ 4).

Crossfield pits. Crossfields of *V. indica* where clearly visible show 1–3 elongated oval pits (text-fig. 3A; Pl. 127, fig. 2). The oval pits are horizontally placed and seemingly simple. On the basis of our observations, we believe that the numerous bordered crossfield pits described by Walton and Wilson (1932) and by Surange and Maheshwari (1962) are pits of tracheidal wall, other than the common wall between a ray cell and a tracheid. In a compression, this wall may overlap a crossfield and then the pits can be mistaken for crossfield pits. The length of the crossfield pits ranges from 11–32 μ (average 18 μ, δ 2) and breadth from 4 to 14 μ (average 5 μ, δ 1).

Phloem like cells. Many pulls show thin elongated cells by the side of xylem which look like phloem (text-fig. 3 C; Pl. 127, fig. 3). The length of these cells is from 17 to 238 μ (average 61 μ, δ 17) and breadth 4–35 μ (average 10 μ, δ 3). The thickness of the walls of these cells is up to 3 μ.

EXPLANATION OF PLATE 126

Figs. 1–5. *Vertebraria indica* Royle. 1, Xylem showing tapering ends of two tracheids and longitudinal walls of others with multiseriate pits, Slide No. 1807A, ×800. 2, Portion of wide tracheid (on the right side) showing six-seriate pits, Slide No. 1807A, ×800. 3, Xylem showing triseriate pits, opposite in some regions but alternate and araucaroid in other parts, Slide No. 1754C, ×350. 4, Pull from thinner axis with obscure rectangular areas showing typical *Vertebraria* type of xylem, Slide No. 1784 Db, ×140. 5, Xylem showing a 7-cell-high ray, Slide No. 1807A, ×200.

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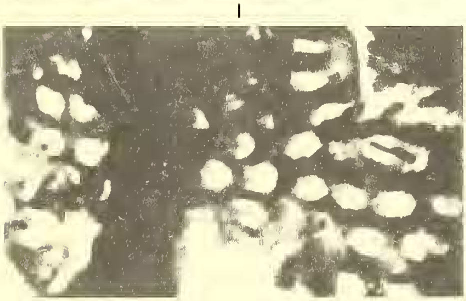

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PANT and SINGH, Permian *Vertebraria*